

THE SHELL STRUCTURE OF CHONETACEAN BRACHIOPODS AND THEIR ANCESTORS

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SYNOPSIS

The criterion of shell microstructure has been added to general morphological considerations in this study of possible ancestors for the Chonetacea. The results support Havlíček's suggestion that the sub-family Aegiromeninae was the plectambonitacean stock from which the first chonetacean evolved in the late Ordovician. Ordovician to Permian chonetaceans have been studied and the observed changes in their shell structure are discussed. Functional morphological interpretations are presented and consideration is given to the significance of spines in these brachiopods.

I. INTRODUCTION

DURING the past ten years or so there have been several notable publications on the Chonetacea. The origin and phylogeny of the group has always been problematical, for, as Muir-Wood wrote in 1962, 'More research requires to be done . . . if the relationship of these very numerous and wide-spread forms is to be established.' She briefly discussed chonetacean origin indicating that she favoured the Plectambonitacea as ancestors, but reminded readers of Paeckelmann's suggestion (1930) that the chonetids were derived from a strophomenid stock.

More recently Boucot & Harper (1968) have revised Silurian and Lower Devonian Chonetacea, but restricted themselves to phylogeny within the group and made no comment upon ancestry. However, Havlíček (1967) while discussing the evolution of the Sowerbyellidae ' . . . assumes *Chonetoidea* to be incontestably the direct precursor of the superfamily Chonetacea . . .'. Havlíček derives *Chonetoidea* from an *Aegiromena* stock whilst *Eochonetes* is derived from the *Sowerbyella* stock. In his view, therefore, *Eochonetes* is not in the group ancestral to the chonetaceans as I had implied in 1968.

Thanks to the stimulus provided by the work of Williams, especially his shell structure study of 1968 which formulated a framework for future research, we are now in a better position to apply detailed examinations of shell microstructure to

the problems of phylogeny in a meaningful fashion. Williams interpreted the shell microstructure of the Chonetidina, Productidina and Strophomenacea as being fundamentally the same, (i.e. entirely laminar) while that of the Plectambonitacea differs in retaining a fibrous secondary layer. In his phylogenetic chart Williams (1968) derived the chonetids, productids and oldhaminids from the Strophomenacea, which in turn, along with the Davidsoniacea and 'probably the triplesiidines' he derived from the Plectambonitacea by a process of neoteny: the laminar shell of the strophomenides being homologized with the laminar primary layer of the plectambonitaceans.

We are left, therefore, with the need to investigate the possibilities of chonetids being derived either from plectambonitaceans involving a change of shell structure, or from the strophomenaceans, with which they appear to have a common shell structure.

Clearly, in any such study the more factors investigated the better. I believe the microstructure of the brachiopod shell to be so intimately bound up with the metabolism of the living organism as to be of profound importance systematically; nevertheless, it is vitally important to consider closely the gross morphology of the valves so as not to suggest evolutionary relationships involving highly improbable morphological changes. The purpose of this study is the detailed investigation of the chonetacean shell microstructure, together with that of their possible ancestors, in the hope of resolving the early phylogeny of this group, the evolution of which took place during Upper Ordovician times.

I retain here the view expressed in 1968 that the Chonetacea should be classified more closely to Productacea than, for instance, to the Strophomenacea. The removal of the Cadomellacea from Muir-Wood's suborder Chonetidina (Cowen & Rudwick 1966) leaves only the Chonetacea, and, at present, I am in favour of leaving the situation fluid to the extent of retaining the Chonetacea as a superfamily within the Strophomenida and not using the term Chonetidina. The Productidina usefully unites several superfamilies which have reasonably established morphological characteristics in common. The Strophomenida as a whole is an order within which there is room for phylogenetic reappraisals, e.g. the removal of *Thecospira* and *Cadomella* (Brunton & MacKinnon, in press), and introduction of the Triplesiacea and Thecideacea, problems upon which several palaeontologists are engaged and have already commented (Cowen & Rudwick 1966, Williams 1968, Rudwick 1968, Wright 1970, Mr. D. MacKinnon personal communication January 1971).

II. MORPHOLOGY

The most recent and complete description of chonetaceans is that of Muir-Wood (1962). Several aspects of their morphology have been discussed (Brunton 1968) but further work now necessitates some revision.

The main point of departure from the views expressed in 1968 concerns the possible reconstruction of the lophophore (1968, text-fig. 50). At that time the traditional idea of a spirolophore for chonetaceans was followed. However, more recent studies on this group, productaceans, strophalosiaceans and thecideaceans

leads to the opinion that the lophophore in these fossil groups consisted of a schizolophe or variously lobed forms of a ptycholophe. In the sense of Williams & Rowell (*in Williams et al* 1965 : H37-8) it is a lobed trocholophe because the lophophore is believed to have had only a single series of filaments, as in Recent *Thecidellina*, rather than the more complex double filaments characteristic of most other Recent lophophores from the schizolophous to plectolophous stages. Rudwick (1968) reminds us that the terminology employed to describe lophophores was based originally upon the arrangement of the brachial axis without consideration for the number of filament rows. Thus whilst phylogenetically there is logic in Williams and Rowell's terminology (1965, H38), it is less confusing to retain the previously existing definitions qualified, where necessary, to indicate if the filament series is double or single. Believing that the thecideaceans may be remnants of the Strophomenida, derived from a productidiniid stock not far removed from *Cooperina* Ternier, Ternier & Pajaud 1967 (but see Cooper & Grant 1969), it is logical to interpret the chonetacean lophophore as having been only a single row of filaments (Text-fig. 1). In his study of the Triassic brachiopods *Thecospira* and *Bactrynum*

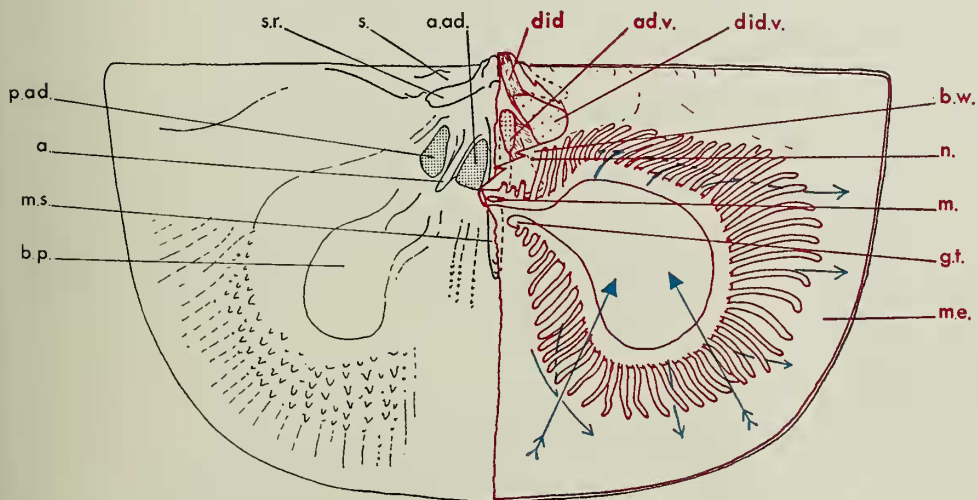


FIG. 1. Diagrammatic dorsal valve interior of a chonetacean showing, on the left, general morphology and, on the right, the inferred anatomy and suggested water currents associated with the lophophore, a. - anterior adductor muscle; a.ad. - anterior adductor muscle scar; ad.v. - adductor muscle, ventral attachment area; b.p. - brachial platform; b.w. - inner epithelium of the body wall separating the brachial cavity from the visceral cavity. The epithelium of the visceral cavity has been cut ventro-medially to expose the muscles; did. - diductor muscle; did.v. - ventral attachment area of the diductor muscle; m. - mouth; m.e. - mantle epithelium; m.s. - median septum; n. - possible position of the nephrostome in the body wall, excreting into the posterior exhalant current; p.ad. - posterior adductor muscle scar; s. - socket; s.r. - socket ridge; \Rightarrow - inhalant and \rightarrow - exhalant feeding/respiratory water currents.

Rudwick (1968) discussed their affinities with the Thecideacea and the general phylogeny of that superfamily. He accepted the Termiers' & Pajaud's (1967) assignment of the Permian genus *Cooperina* to the Thecideacea, so that it became the earliest representative of the superfamily, which he considered as derived from a Lower Permian or even earlier davidsoniacean. Study of *Cooperina* shows that Cooper & Grant (1969) are correct in placing the genus in the Strophalosiacea and it seems that the morphological evidence presented by Rudwick for a derivation from the Davidsoniacea is better met by the Strophalosiacea, a group believed to have diversified widely and to have given rise to both the Richthofeniacea and Lyttoniacea. Rudwick (1968, 1970) related the Lyttoniacea and Thecideacea to the Davidsoniacea.

While preparing this paper I was privileged to be shown the script of a paper by Grant (in press) in which he describes a calcified 'ptycholophous brachiophore' in Permian Productidina (ptycholophous here used as by Grant in the morphological sense of being several lobed). The interpretation of this structure supports the contention that the brachial ridges of Productidina do indeed mark the positions to which the lophophore was attached in the living animal and that the 'ptycholophous' (or multilobed trocholophous) lophophore described by Grant evolved as a specialization from the more generalized schizolophe or simple ptycholophe characteristic of many Strophomenida.

A study of particularly well preserved Pennsylvanian and Permian chonetacean interiors in the collections of the National Museum of Natural History, Smithsonian Institution, Washington, shows that in some rugosochonetids and species of *Dyoros* the antero-median tuberculation of the brachial ridges merges into the anterior end of the median septum. In some thickened (? old) specimens of *Dyoros* the anterior end of the median septum is winged laterally in such a way as almost to bridge the gap between it and the brachial ridges (Text-fig. 2). The exaggerated development of tubercles and prolonged deposition of secondary shell in the regions of the brachial

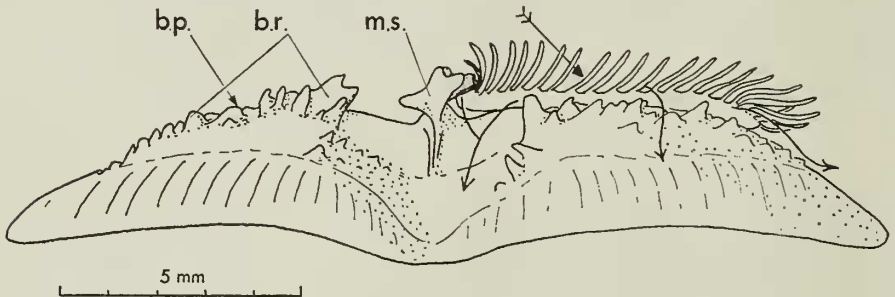


FIG. 2. Anterior view of *Dyoros* sp. (Chonetacea) dorsal valve from the Permian of Texas illustrating the highly tuberculate brachial ridges and anteriorly winged median septum. The inferred position of the lophophore and feeding water currents are added on the right. → inhalant current; ⇨ exhalant current; b.p. - brachial platform; b.r. brachial ridge, m.s. - median septum.

ridges and median septum probably resulted from the stresses imposed by the lophophore upon the secretory mantle epithelium in these areas. It may have been simply the weight of the lophophore hanging from the dorsal valve that induced this additional shell secretion in those specimens living in a position with their dorsal valves uppermost.

The chonetacean lophophore is envisaged as having been suspended from the dorsal inner epithelium with the postero-median mouth segment attached to the body wall between and probably ventral to its support by the anterior tips of the anderidia (= lateral septa of Muir-Wood 1962). The strong tuberculation of the brachial ridges probably reflects the strong attachment of the mantle to the shell where it supports the lophophore (Text-fig. 3). Antero-medially the generative tips of the lophophore probably recurved posteriorly onto the median septum (Text-fig. 1); however, it is impossible to say whether they remained separated by the septum or united in the median plane as in living *Megathiris*.

The relationship between pseudopunctae and taleolae requires clarification. In the brachiopod volume of the Treatise (1965 : H420) Muir-Wood incorrectly redefined the term taleolae, specifically as applied to chonetids, saying that they had a 'central cavity'. In observing many taleolae under the scanning electron microscope a central cavity has never been observed. It may be that the impression of such a structure resulted from optical effects or that the cavities were those of rib apertures.

Taleolae, as defined by Williams (1956), are rods of calcite in the axial position of many pseudopunctae (Pl. 1 figs 1, 2). Taleolae are found neither in all pseudopunctae nor necessarily forming the core to the complete pseudopunctum in which they occur. When absent the shell layers or fibres can be traced into the centre of the structure, which is composed of inwardly and commonly anteriorly directed conical flexures producing tubercles on the inner surfaces of the valves (Pl. 1, fig. 4). This structure contrasts with the outward flexures of shell fabric surrounding endopunctae (Brunton 1969, fig. 11, 1971; pl. 11, figs 8, 10). The pseudopunctae of upper Palaeozoic chonetaceans have taleolae while those of geologically older specimens are without, or with only weakly developed taleolae. Baker (1970) describes *Moorellina* specimens within which the pseudopunctae differ in character; those of the dorsal valve have cores of primary shell resembling taleolae, whilst those of the ventral valve are without and composed entirely of radially disposed bundles of secondary fibres.

In 1968 the author's text-figure 45 indicated that he interpreted the sub-median ridges in the ventral valves of some chonetids as being the traces of mantle canals. It is now believed that in some narrow-bodied species with thickened shell these ridges developed in the regions bordering the ventral edge of the dorsal median septum. In such specimens the brachial cavity of the closed shell would have been divided almost completely into two chambers. The significance of this is not clear and the relationship of these ridges to mantle canal traces is in doubt; the effect, however, is similar to that of mantle canals, viz. the pressure of a structure onto the internal epithelial surface inhibiting shell deposition with increased shell thickening on either side.

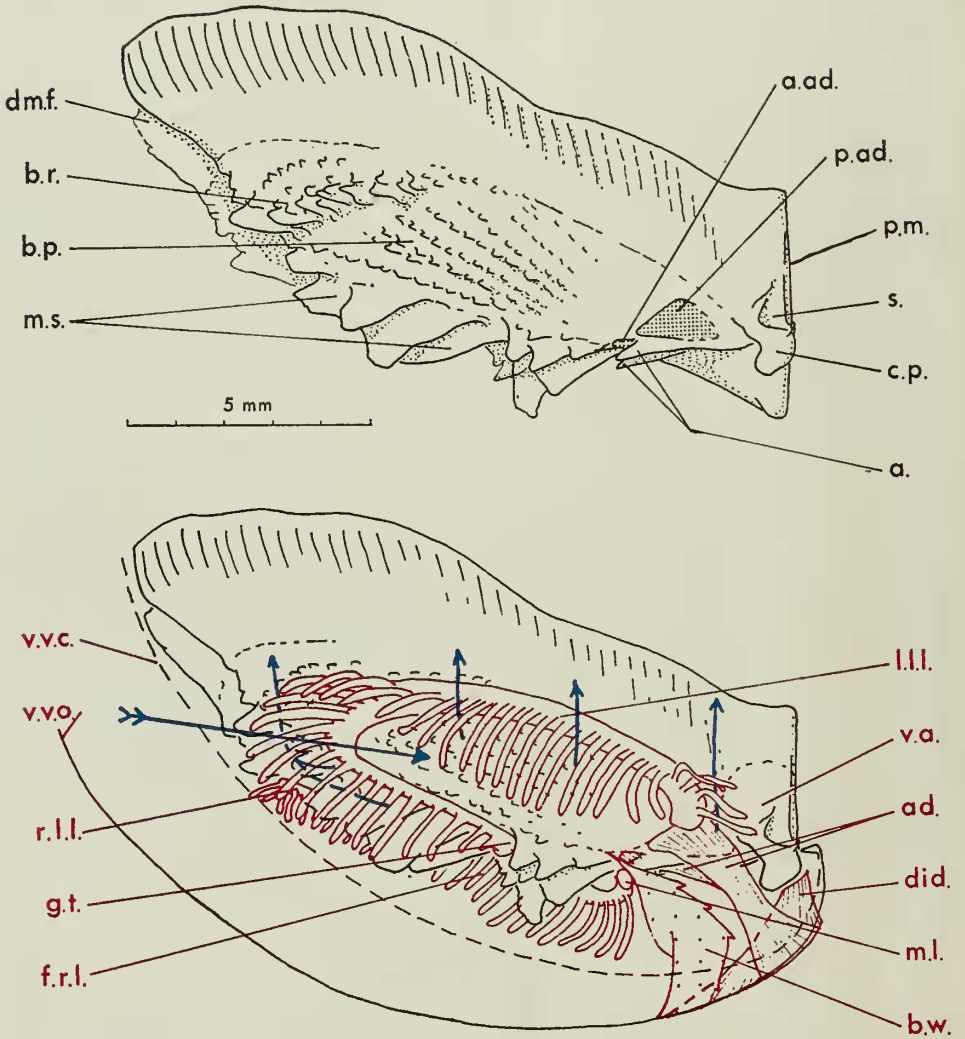


FIG. 3A. Ventro-lateral perspective view of the dorsal valve interior of *Dyoros* sp. from the Permian of Texas illustrating the surface morphology.

a. - anterior end; a.ad. - anterior adductor scar; b.p. - brachial platform; b.r. - brachial ridge; c.p. - cardinal process; dm.f. - dorso-median fold; m.s. - median septum (here strongly tuberculate); p.ad. - posterior adductor scar; p.m. - posterior margin of valve; s. - socket.

If one ignores the Daviesiellidae, in particular *Daviesiella* and *Airtonia*, and *Chonostrophia* (which may not be a chonetacean) the Chonetacea are morphologically conservative from their origins in the Upper Ordovician to the topmost Permian. Normally they share a gently concavo-convex profile, multicostellate ribbing, low interareas set at a wide angle from each other and several pairs of more or less posteriorly directed hollow spines on the posterior margin of the ventral valve. Teeth, sockets and socket ridges are developed, and in the dorsal valve the adductor scars commonly are divided by a ridge (anderidia). The cardinal process is low, internally bilobed in early forms but tending to become knob-like and commonly trifid externally; the median septum is only high anteriorly and developed late in ontogeny. The pseudopunctate shell manifests itself internally by tubercules. At least in early stages of ontogeny several genera were attached to the substrate by a thin apical pedicle protected by a shelly sheath.

III. ANCESTRAL STOCKS

At first sight certain strophomenaceans seem suitable as ancestors to the Chonetacea; general shape and size of some stropheodontids seem correct, as are features such as the dorsal valve protugal node and development of a pedicle sheath on such genera as *Pholidostrophia*. Williams' 1968 investigations indicated that the shell structure is comparable in both groups, i.e., essentially laminar. However, it is shown below that the shell structures differ and the above characteristics are common to the Strophomenida.

Previous morphological studies have shown that many features are shared by the Plectambonitacea and Chonetacea with the result that several palaeontologists (e.g. Chao 1928, Sarycheva & Sokolskaya 1959, Muir-Wood 1962, Havlíček 1967) have thought these superfamilies to be phylogenetically related.

Strophomenacea, Plectambonitacea and Chonetacea obviously share strophomenid characteristics, but whilst doing so certain features of the Chonetacea tend to be more akin to those of the Plectambonitacea, especially the Sowerbyellidae, than to the Strophomenacea. Thus the Sowerbyellidae and Chonetacea share similar shell profiles and outlines and do not include the same elaboration of shell shapes met

FIG. 3B. Inferred principal anatomy added to the above specimen (in red) and possible ciliary induced water-current through the lophophore (in blue). \gg Inhalant current; exhalant current; ad. – adductor muscle, divided dorsally by anderidium; b.w. – body wall with left side removed to expose visceral cavity; did. – diductor muscle; f.r.l. – filaments of right lophophore lobe; g.t. – generative tip of lophophore; l.l.l. – left lobe of lophophore; m.l. – mouth (median) segment of lophophore, cut on left to expose muscle bases; r.l.l. – right lobe of lophophore; v.a. – left visceral region; v.v.c. – position of the interior of the ventral valve when the shell was closed; v.v.o. – inferred relative position of the ventral valve when the shell was open by about 20°. N.B. This reconstruction is not intended to imply a ventral movement of the ventral valve when the shell opened. Other than a portion of the body wall, epithelial layers, such as the mantles, are not depicted and it should be remembered that epithelia would have covered all the internal shell surfaces illustrated.

within the Strophomenacea. Similarly with external ornamentation, save that accentuated costae common to several sowerbyellid genera are only hinted at in the oldest chonetacean genus, *Strophochonetes*.

Early and mid-Ordovician Plectambonitacea are more varied in shell shape and it seems that the Strophomenacea inherited this tendency to variety. By upper Ordovician times shell shape was more stable in Plectambonitacea and from such a stock the Chonetacea inherited their conservative outline and profile.

Within the dorsal valves of sowerbyellids are paired ridges lateral to the mid-line or median septum, which is low or absent posteriorly leaving a cavity at the base of the cardinal process; a cavity interpreted as that of the brephic valve. These features are more common to the chonetaceans than to strophomenaceans. In Plectambonitacea the ridges ('inner' and 'outer side septa' and 'bema' of Cocks 1970) may be homologized with the anderidia, accessory septa and brachial ridges of chonetaceans. The pit at the base of the cardinal process is the alveolus of chonetaceans.

Whilst some Strophomenacea share some of these features, as well as denticulate hinge lines, their general combination is more in keeping with Sowerbyellidae and Chonetacea. Furthermore, some mid- and upper Ordovician Sowerbyellidae, e.g. *Eochonetes*, *Chonetoidea*, possibly *Sentolunia*, have hollow canals in the ventral valve posterior margin which are closely comparable to the spine canals of chonetaceans. Havlíček (1967 : 38) suggested that these canals may have accommodated hold-fasts used to attach these plectambonitaceans to seaweed.

On looking at mid- to upper Ordovician faunas for possible chonetacean ancestors it seems that the morphological requirements may best be met by the Sowerbyellidae.

IV. PLECTAMBONITACEA

Since this study was started Cocks has published on Silurian Plectambonitacea (1970). His paper contains useful and interesting discussion on functional morphology, but not all his suggested reconstructions of the musculature and feeding mechanisms are accepted here. These operations have important implications upon the way in which the plectambonitacean/chonetacean shells are envisaged as having been organized. Whilst agreeing to the possibility of the shells being able to snap shut as a defence mechanism and possibly also as a repositioning mechanism, it is difficult to envisage a brachiopod habitually feeding by pumping water through its brachial cavity by means of a flapping valve system such as proposed by Rudwick (1961) for Richthofenacea and invoked by Cocks. A ciliary induced water current seems to be a well tried, stable and energy conserving system widely used in invertebrates and invariably used in extant brachiopods. By whatever means a water current is produced its function is to provide for respiration and feeding. Evidence suggests that a lophophore is required for these purposes, even allowing for the possibility of feeding on dissolved nutrients as proposed by McCammon (1969) and it seems likely that the plectambonitaceans, even the structurally specialized *Eoplectodonta*, retained a lophophore capable of a normal ciliary beat.

It may be unwise to compare a living genus so widely separated from the

Plectambonitacea taxonomically, but the dorsal internal morphology of *Megathiris* has, what are believed to be, analogous structures. In *Megathiris* the quadrilobed ptycholophe, with a single series of filaments, is supported by a calcareous loop partially fused to three ridge-like pillars which are prominent anteriorly. The loop, and thus the lophophore, is a few millimetres behind the anterior faces of these ridges (see Treatise 1965, H 836 for fig.). The lophophore does not project posteriorly along these ridges to the extent that might be supposed from Atkins' figure 6 (1960, - her figure 7 gives a clearer impression of the true situation) which is reproduced in the Treatise (Williams *et al* 1965, fig. 41). The body wall, behind which the muscles and viscera are situated, extends antero-dorsally between these ridges as a dissected plane at approximately 45° to the commissural plane and following the postero-dorsal side of the loop. In this way the anteriorly exaggerated median septum and pair of ridge-like pillars lift the lophophore from the dorsal valve floor allowing the antero-median extension of the body cavity, including dorsal adductor muscles. It is thought that the plectambonitacean morphology, exemplified by *Eoplectodonta*, achieved similar results.

The socket ridges, of Williams, or clavicular plates, of Cocks (1970) are considered to have functioned as postero-lateral supports to the body wall in the region of the mouth segment of the lophophore, much as were the opinions of Kozłowski (1929) and Öpik (1933), (As the principal points of pivot in these shells occurred at the posteromedian surfaces of these structures the term socket ridge is favoured). In this respect *Eoplectodonta* displays a feature common to many of the articulate brachiopods, that of a close relationship between articulation and support of the body wall in the region of the lophophore.

The plectambonitacean lophophore probably followed the lateral edges of the bema (Cocks), or lophophore platform (Williams), so that a variously modified ptycholophe, in which the generative zone (or zones) recurved postero-medianly, was suspended from the dorsal mantle. Assuming a ciliary induced water current from the brachial lip across the filamentous area of the lophophore, a circulation may have been achieved in which water entered ventrally, perhaps particularly medianly, and passed out dorsally, close to the dorsal valve and especially laterally (Text-fig. 4). There seems little good reason why many of the later plectambonitaceans, those that had reduced their teeth, could not have had a wide gape while feeding. A wide gape might be advanced as the reason for very large, anteriorly extended, dorsal adductor muscle scars (Text-fig. 5), rather as is the situation in *Megathiris* today, which opens to about 45° or *Thecidellina* opening more than 60° . Whether or not the dorsal adductor scars of *Eoplectodonta* covered the bema, as suggested by Cocks (1970), it seems clear that these areas and those between the two pairs of septa on the dorsal valve, accommodated body tissues and that the lophophore was elevated on these septa. However, as in *Megathiris*, the lophophore probably did not follow the septal crests because in heavily thickened shells the septa may touch the interior of the ventral valve when the shell is closed, leaving little or no space for the brachial axis.

The morphology of the geologically older (Ordovician) plectambonitaceans is indicative of a schizolophe and perhaps only in geologically younger members of

the Sowerbyellidae did the lophophore evolve into a quadrilobed structure.

In various Ordovician species of *Anoptambonites* and *Bimuria* there is muscle scar evidence for the dorsal adductors being restricted posteriorly, in a more traditional position, and these scars are divided by raised areas which may be homologized with Cocks' 'outer side septa' and possibly with the anderidia of chonetaceans.

It is believed that the Sowerbyellidae, particularly *Eoplectodonta* and *Plectodonta*, were specialized plectambonitaceans which nevertheless retained essentially normal systems of feeding. Their 'cousins', the Aegiromeninae remained more generalized and are morphologically more suitable to have provided the stock from which chonetaceans evolved.

The Aegiromeninae tend to be small-sized shells, commonly about 10 mm. wide, gently concavo-convex with shorter interareas and more regular ribbing than the Sowerbyellinae. Socket ridges are reduced and the dorsal median septum does not extend posteriorly to the cardinal process but appears to be flanked by the adductor

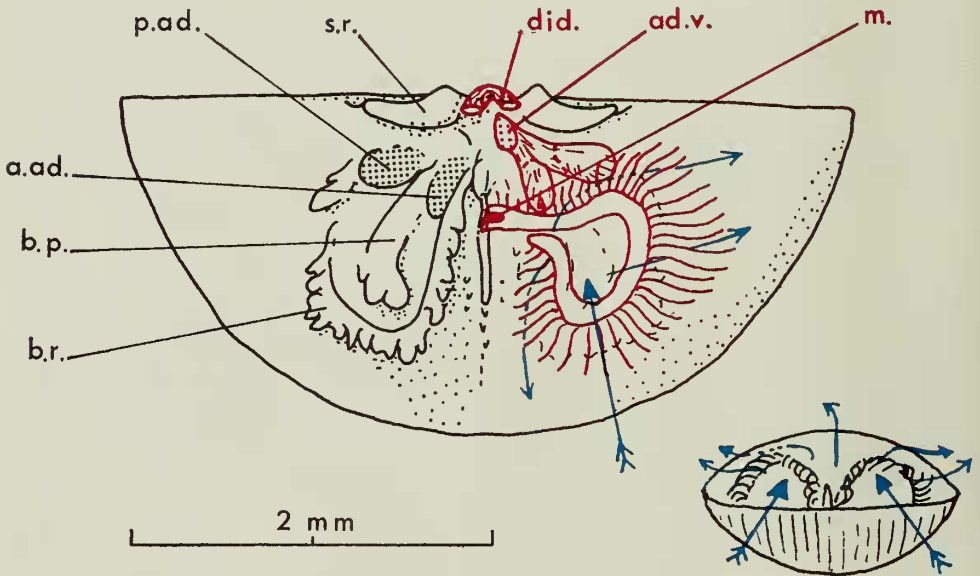


FIG. 4. Stylized illustration, based on *Bimuria siphonata* Cooper, from the mid-Ordovician of Pratt Ferry, Alabama, showing the internal dorsal valve morphology on the left with the inferred lophophore and main muscles on the right (red). The blue arrows indicate the main circulation of water through the lophophore, and this is further illustrated by the small diagram of an open shell, viewed posteriorly, on the right. (The dorsal valve is uppermost and water enters from the front) a.ad. - anterior adductor scar; ad.v. - ventral attachment area of adductor muscle; b.p. - brachial platform; b.r. - brachial ridge; did. - diductor muscle; m. - mouth; p.ad. - posterior adductor scar; s.r. - socket ridge.

muscle scars and variously placed elongate tubercles which may have assisted in the support of the lophophore. There is a complete lack of the strong dorsal internal ridging typical of the Sowerbyellinae and Leptellinidae and this morphology is entirely suitable as being ancestral to the sparsely featured early chonetacean dorsal interiors.

V. SHELL STRUCTURE

Plectambonitacea

Morphologically the Sowerbyellinae form a closely knit subfamily. The shell structure of the genera investigated (*Sowerbyella*, *Viruella*, *Eoplectodonta*, *Thaerodonta*, *Plectodonta* and *Eochonetes*) supports this unity. In these genera the secondary shell layer is standard in that the fibres show an internal mosaic (Pl. 1, fig. 4) and the typical cross-sectional stacking (Pl. 2, figs 1, 2) familiar within Recent terebratulids and rhynchonellids. The outer primary layer appears to be more variable, thin and commonly poorly preserved, and may be differentiated simply as a layer of much smaller 'fibres' (Pl. 2; figs 3, 6). These outer elements do not seem to show the brick-like cross-section or lateral fusion that would be expected in a lamellose fabric. Taleolae are not strongly developed in the pseudopunctae of these shells.

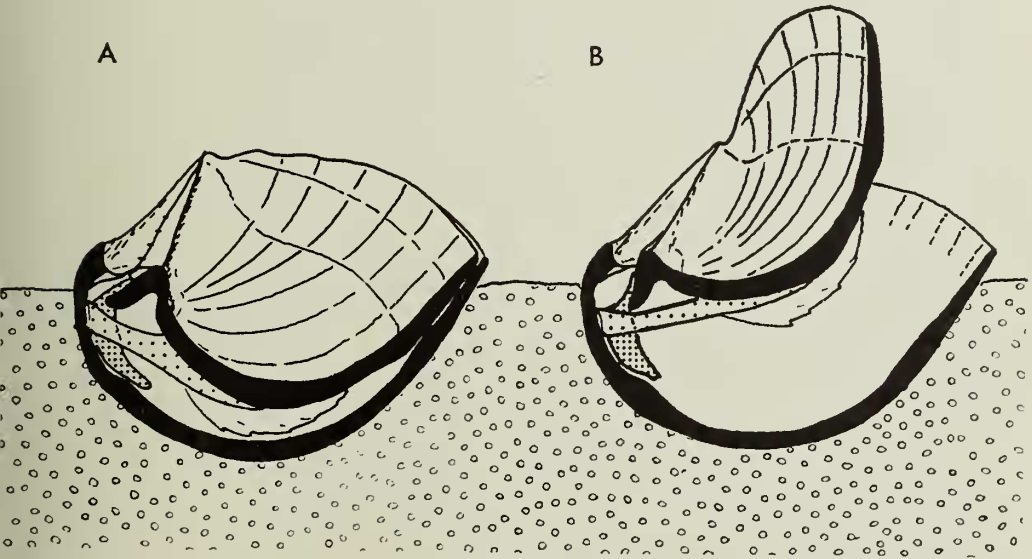


FIG. 5. Median longitudinal section of *Eoplectodonta* showing the inferred adductor and diductor muscles as they might have been when the shell was shut (5A) and open with a gape of 45° (5B). The ventral attachment area of the adductor muscle (coarse stippling) is close to the median plane whilst the dorsal attachment area is between the submedian septum (or inner side septum), here omitted, and the outer side septum, seen beyond the muscle.

An unexpected structure shows in the shell of particularly well preserved *Eoplectodonia transversalis* (Dalman) specimens from the uppermost Llandovery of Gotland. The pseudopunctate secondary layer also has small endopuncta-like canals of about $3\ \mu\text{m}$ diameter surrounded by small outward deflections of the fibres producing a cone-in-cone structure (Pl. 3, figs 2, 3) contrasting with that of the pseudopunctae. It is not yet known to what extent these small endopuncta-like structures pervade the shell and it has only been possible to trace any one of them over a distance of about $80\ \mu\text{m}$ through the secondary layer. They run subparallel to the pseudopunctae and it seems, therefore, that they were controlled by anteriorly migrating points of outer epithelium as distinct from the fixed positions of caeca around which the epithelium moved.

The subfamily Aegiromeninae seems rather more varied in its shell structure, as judged by evidence from *Aegiromena*, *Aegiria* and *Sericoidea*. Within this subfamily the shell structure differs from other Sowerbyellidae.

In *Aegiromena aquila* (Barrande), from the middle Ordovician of Czechoslovakia, the secondary shell is not entirely composed of standard fibres. Whilst retaining a well-separated, independent appearance, as if having been encased within organic sheaths during life, the typical fibre cross-sectional shape has almost been lost; only in rare instances (Pl. 3, fig. 5) can such fibres be distinguished and these tend to be towards the outer surfaces of the valves i.e. they were formed at early stages in the growth of the shell. Normally the fibres are about $14\ \mu\text{m}$ wide and elliptical in cross-section, their edges overlapping adjacent fibres to various extents (Pl. 3, fig. 5). The shell fabric is strongly pseudopunctate and these normally have taleolae (Pl. 4, figs 1, 2). Towards the external surface of valves the fibres are of a slightly smaller dimensions and tend to be thinner. A strongly differentiated primary layer has not been recognized, if indeed it ever existed, but these smaller external fibres may indicate a gradation from a thin laminar primary layer to the fibrous secondary layer.

Aegiria grayi (Davidson) from the Wenlock Shales of Dudley, England, is sparsely pseudopunctate and the fibres of the secondary layer retain a rather more standard appearance (Pl. 4, fig. 3). In these respects the species is somewhat more akin to the Sowerbyellinae, but the general morphology would not warrant a change to this subfamily. Primary shell was not distinguished in the material studied.

In *Sericoidea restricta* (Hadding) from the Caradoc of Girvan, Scotland, the sparsely pseudopunctate secondary layer shows virtually no sign of retaining standard fibres. The 'fibre' units within the shell appear to be well separated, as if formed in the standard manner within organic sheaths, and are of comparable dimensions ($25\text{--}30\ \mu\text{m}$ wide and $3\text{--}4\ \mu\text{m}$ thick). Orientation of the 'fibres' remains subparallel from layer to layer (Pl. 4, fig. 4, Pl. 5, fig. 1), thus retaining the organization of the standard regime rather than the marked alteration in the orientation of blades in adjacent sheets typical of many Strophomenida (see Armstrong 1969). Again, a well-differentiated primary layer has not been discovered unequivocally. Recrystallization is most common at the shell surfaces and pressure solution of the enclosing sediments interferes with the external shell fabrics. However, over certain areas of the valve's exterior a layer of small laminae

can be seen (Pl. 5, fig. 2). These are only 3–4 μm wide, appear to grade within one or two layers into the full-sized fibres, and probably constitute a remnant primary layer.

We have, therefore, within the Aegiromeninae a differentiation of at least the secondary shell layer away from the standard parallel fibrous fabric typical of geologically older plectambonitaceans (*Ahtiella*, *Inversella*, *Toquimia*, *Leptestia*, *Leptelloidea*, and *Bilobia*), genera studied to demonstrate the standard nature of the early plectambonitaceans (Pl. 5, figs. 3, 4) and which continued on within the Sowerbyellinae. *Ptychoglyptus* and *Xenambonites* have not been studied.

It is Havlíček's opinion (1969 : 38) that the sub-family Aegiromeninae is the group from which chonetaceans evolved. Further, he assumed '*Chonetoidea* to be incontestably the direct precursor of the superfamily Chonetacea in which canals extended posteriorly into long hollow spines'. Unfortunately it has been impossible to find *Chonetoidea* specimens suitably preserved for the study of their shell, but morphological considerations support Havlíček's opinion that *Chonetoidea* evolved from a *Sericoidea*-like ancestor.

It is necessary, therefore, to test this suggested phylogeny against the shell structure of the oldest known chonetaceans. The oldest undoubted species is *Chonetes* (*Eochonetes*) *primigenius* Twenhofel (1914) from Anticosti Island, Canada. Twenhofel recorded the species from four formations, the Charleton (\equiv Vauréal) and Ellis Bay Formations of Richmond (high Ordovician) age, and the Gun River and Jupiter River Formations of Lower Silurian age. The holotype was figured from the Gun River Formation and a ventral valve exterior figured from the Charleton (Vauréal) Formation. It is still generally agreed that the Ellis Bay Formation is uppermost Ordovician in age. Dr. O. A. Dixon has been kind enough to send rock samples with this species from Mile 5, Juniper River and Mile 2 47 Mile Road, Anticosti, from the Ellis Bay Formation. Amongst these are several examples of dorsal valve interiors (Pl. 5, figs 5–8), figured for the first time here, and the shell substance is reasonably well preserved in the ventral valves. The species was assigned by Muir-Wood (1962) to her new genus *Strophochonetes*. Boucot & Harper (1968) called into question the validity of both *Strophochonetes* and *Protochonetes* of Muir-Wood (1963). A study of Lindström's specimens of *Strophochonetes cingulatus* (in the BM(NH) collections and used by Muir-Wood in defining the genus) and of *Protochonetes ludloviensis* Muir-Wood, type species of that genus, together with specimens of *P. striatellus* (Dalman) from the Wenlock of Gotland, a species very close to *ludloviensis*, convinces me of the separate identity of the two genera. In the author's experience unabraded *S. cingulatus* and *S. primigenius* specimens always have a ventral median accentuated rib. The outline is relatively less wide than in *Protochonetes ludloviensis* or *P. striatellus*, and whilst spines may be abundant on *Strophochonetes* (up to at least seven pairs) they extend more or less perpendicularly from the valve margin. Those of *Protochonetes* extend postero-laterally. A divided ventral median septum in *Strophochonetes* has never been observed.

It is perhaps significant that a collection, as yet undescribed, made by Dr. Cocks from the low Wenlock Knockgardner Beds of Girvan, Scotland, includes many

chonetacean specimens which appear to show characteristics intermediate between those of the types of *Strophochonetes* and *Protochonetes*. The specimens are small, approximately 10 mm. wide, and in outline resemble *Protochonetes*; the ribbing is even but the ventral median septum is ill defined posteriorly. Spines seem to be variably disposed, some nearly perpendicular, others at an angle to the hinge line.

Chonetacea

The shell of *S. primigenius* is characterized by its parallel to subparallel arrangement of fibre-like elements (Pl. 6, fig. 1, 2) which both overlap adjacent fibres laterally and, in other parts of the shell, abut to their neighbouring fibres with a more or less perpendicular plane of separation. Whilst the packing of these fibres is tight, they retain a discreteness and do not show signs of having fused laterally with adjacent units, as is the situation in the bladed and sheet fabrics of Armstrong (1969) or truly laminar fabrics of Williams (1968, 1970). These lath-like fibres are 6 to 10 μm wide and of variable thickness, but commonly between 2 and 4 μm thick. Pseudopunctae are sparsely developed in ventral valves (Pl. 6, fig. 1), but judging from the dorsal valve internal tuberculation pseudopunctae are more common in this valve.

A clearly differentiated primary layer has not been recognized, but towards the exterior of the valves the fibres have the appearance of Williams' 'crested lamellae' (1968 Pl. 21, figs 2, 4). In *Strophochonetes* this structure may result from slight recrystallization of the outermost shell layers.

The seemingly separate nature of the shell 'fibres' and lack of sheet fabrics leads to the conclusion that the shell was laid down essentially in the standard way as proposed by Williams (1956, 1968), that is by individual outer epithelial cells secreting the calcite for individual fibres which were separated from one another by organic sheaths.

Other chonetacean records from Ordovician rocks are unsatisfactory. Study of the specimens recently referred to by Lister, Cocks & Rushton (1970) from upper Ordovician rocks of the Bobbing Bore, Kent indicates that they probably are chonetaceans. However, preservation is poor and the shell material is lacking or altered. Reed (1944) described a new species, *Chonetes (Eochonetes) celtica*, from the Upper Ordovician Balclatchie Beds of Ayrshire, Scotland, which was assigned to *Strophochonetes* by Muir-Wood (1962). Neither spines nor spine bases can be seen on the holotype in the Hunterian Museum, Glasgow and the acutely angular relationship of the interareas is much more suggestive of a plectambonitacean than a chonetacean.

From Middle Llandovery rocks of Newlands, Girvan, Scotland Dr. Cocks has found two ventral valves of a *Strophochonetes* species showing spines, but no shell is preserved. By mid-Silurian times chonetaceans were becoming more abundant, but their main diversification did not take place until the Upper Palaeozoic during which first the Plectambonitacea and then the Strophomenacea died out.

In addition to *Strophochonetes* the following chonetaceans have been studied for shell structure: *Protochonetes striatellus* (Dalman) from the mid Silurian of Gotland,

from where also comes a small chonetacean species, possibly *Eoplicanoplia* Boucot & Harper 1968; *P. ludloviensis* Muir-Wood from Upper Ludlow rocks of Eastnor, Hertfordshire; *Dawsonelloides canadensis* (Billings) from Lower Devonian rocks of Gaspé, Quebec; *Retichonetes vicinus* (Castelnau) from mid-Devonian Arkona shale of Ontario; *Rugosochonetes* species from Lower Carboniferous strata of County Fermanagh, N. Ireland; Mississippian of Oklahoma, and basal Namurian of Northumberland; *Neochonetes* from the Permian of Texas, USA, and specimens from the Permian of Russia.

In general the shell fabric of these later chonetaceans supports that seen in *S. primigenius*. Pseudopunctuation, including well differentiated taleolae, became more strongly developed by the lower Devonian (Pl. 7, figs. 1, 3) and continued within the stock. The greater part of the shell thickness retained a lath-like fibrous nature (Pl. 7, figs 1, 2), although each 'fibre' was only from 2–4 μm wide and up to about 1 μm thick, until the early Devonian when there are clear signs of lateral fusion of 'fibres' (Pl. 7, fig. 3) into units 8–10 μm wide. In lower Carboniferous specimens, such as *R. silleesi* Brunton, while lath-like units are readily distinguishable throughout much of the shell their orientation from layer to layer is variable (Pl. 7, fig. 4) and towards external surfaces sheets of blades are developed (Pl. 8, figs 1, 2) into what approaches a true cross-bladed fabric (Pl. 8, fig. 3).

Thus it seems that a trend away from the typical fibrous secondary shell of many Ordovician Plectambonitacea can be traced through members of the Aegiromeninae into the earliest known chonetaceans of the Lower Palaeozoic and on into the Upper Palaeozoic when chonetaceans were at their most abundant and diverse (Text-fig. 6). It seems, therefore, that within the Chonetacea the laminar shell fabric, like that of the Strophomenida other than the Plectambonitacea, developed independently from that in the Strophomenacea which, in Williams' (1970) view, arose from a Cambro-Ordovician plectambonitacean-like ancestor derived from the nisusiid Billingsellacea (Text-fig. 7). This change in shell structure involved a reduction in the size of fibres indicating a reduction in the size of the secretory outer epithelial cells. This trend continued in the early chonetaceans, along with a loss in regularity and consistency in growth direction of the fibres at any one time or at different times during ontogeny. This may have resulted from the increased development of pseudopunctæ to which small areas of specialized epithelium became fixed. In this way local areas of epithelium may have been retarded in their general anterior growth, so distorting the uniformity of calcite secretion in adjacent areas. Furthermore, an increasingly mobile epithelium, in terms of periodic retraction from the valve edges, would have resulted in the likelihood of renewed forward growth taking place in slightly altered directions and consequently the non-alignment of new fibres.

If the development of all laminar shell is as inferred by Williams (1968) for *Juresania* then a continued reduction in epithelial cell size did not continue. In Williams' view a single epithelial cell (implied by his text-fig. 25 as being about 12 μm wide) secreted several blades, each to some extent separated by impersistent proteinous strands and abutting laterally to form more or less continuous sheets. The alternative is for each blade to have been secreted from single epithelial cells, in

the case of Devonian and Carboniferous chonetaceans between 2 and 5 μm wide, which progressively ceased to produce the protein sheets which separate normal fibres. But in whatever way laminar shell was deposited it is clear that the epithelium was unusually mobile by modern standards (Brunton 1969), and that the proteinous strands and old cell boundaries were ruptured at times of mantle regression. At such times the regressing epithelial cells probably laid down a proteinous sheet continuous with the periostracum. During transgressive renewed

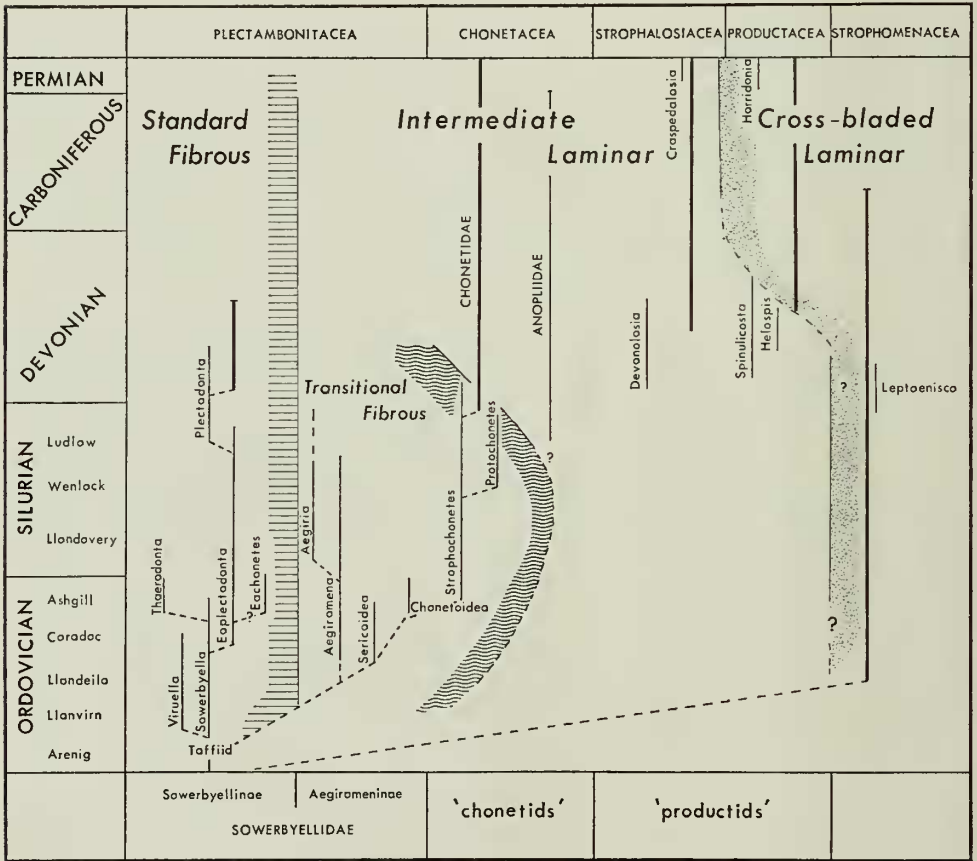


FIG. 6. Inferred phylogenetic relationships between those genera of the Plectambonitacea and Chonetacea in which shell microstructure has been studied. Those taxa in which the name is horizontal have not been studied in detail. Principal features of the secondary layer shell fabric are differentiated and labelled in italic script. Five productid genera are included to indicate the results of preliminary investigations on their shell structure and relationships. It is suggested that the plectambonitacean to chonetacean changes in shell structure may have continued and given rise to the productids. *Leptaenisca*, commonly cited as ancestral to the Productacea, would seem not to have a typically strophomenacean shell of cross-bladed laminae.

calcite deposition these proteinous layers would have become entombed within the shell fabric and consequently separated one skeletal sheet from another so accentuating the lamination typical of this type of brachiopod shell fabric.

Preliminary results from the investigation of mid-Devonian productacean and strophalosiacean shell microstructures shows them to be composed of semi-parallel lath-like units 2–3 μm wide with little development of laminar sheets (Pl. 8, fig. 4, Pl. 9, fig. 1), whilst Carboniferous and Permian productaceans have typical cross-bladed fabrics (Pl. 9, figs 2–4). Such fabrics may be explained as a continuation of the evolutionary trend outlined above, but further study is in progress on this

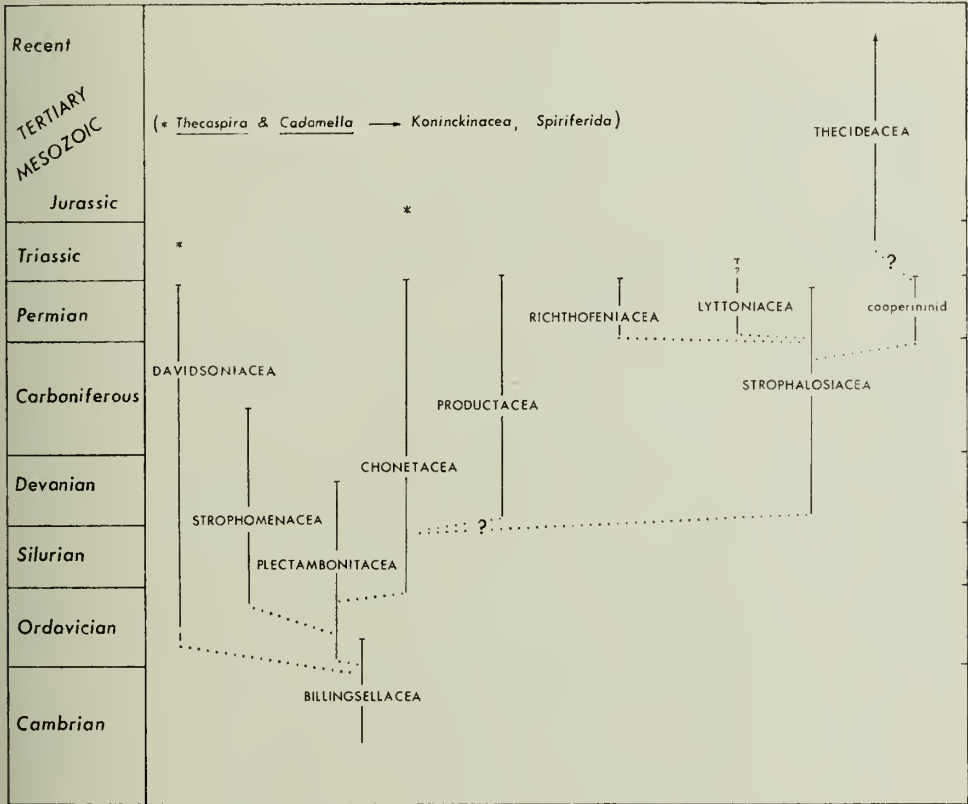


FIG. 7. Speculative phylogeny of certain superfamilies of the Strophomenida, together with their ancestral stock, the Billingsellacea. The strophalosiacean *Cooperina*-like group may be close to the stock from which the Thecideacea arose. Pseudopunctuation was developed within the Davidsoniacea and at the start of the Plectambonitacea. Endopunctuation developed in the Thecideacea, possibly early in the Jurassic. (**Thecaspira* and *Cadomella* have been placed in the Davidsoniacea and Chonetacea respectively. It is thought likely that they belong to the spiriferide Koninckinaea).

question and the more traditional derivation of these stocks, via *Leptaenisca*, from the Strophomenacea may yet prove possible. Study of two imperfectly preserved specimens from the Haragan Shale of Oklahoma shows that the shell fabric of *Leptaenisca* is not truly laminar. The genus can not, therefore, be excluded from possible productidine ancestral stocks by reason of its shell alone. The shell of Permian strophalosiaceans appear to have retained a less laminar shell than productaceans.

VI. DISCUSSION AND CONCLUSIONS

This study, based upon shell microstructure, supports Havlíček's conclusions, based upon morphology and stratigraphy, that the family Chonetacea was derived from aegiromeninid Plectambonitacea.

Ordovician plectambonitaceans have a shell structure with small 'fibres' (possibly equivalent to the 'laminae' of Williams 1968) about 6 μm wide in the outer layer, which grade rapidly into a normal parallel-fibrous shell fabric similar to that of Recent brachiopods. This gradational change may simply be a reflection of the increase in size of epithelial cells away from the mantle edges; a possibility which cannot be tested without studying well preserved and undamaged shell margins. Within the mid-Ordovician to Silurian aegiromeninid Plectambonitacea a progressive change occurred which links the shell structure of this subfamily to that of the earliest known chonetaceans in the uppermost Ordovician.

Like some aegiromeninids, the lower Palaeozoic chonetaceans have a shell composed of small lath-like fibres which retain their individuality, in contrast to the sheet structures that began to develop in Upper Palaeozoic specimens.

The internal morphology of aegiromeninids, particularly that of the dorsal valve, is simpler than that of most other plectambonitaceans. Within the subfamily various morphological features were 'tried', some of which may be homologous to chonetacean characteristics, and Havlíček (1967) suggested that some genera altered their way of life from benthonic to epiplanktonic, being attached to floating algae. Thus it was a group undergoing much evolutionary change.

The socket ridges of Sowerbyellinae extend antero-laterally and probably assisted in the support of the body wall. In the Aegiromeninae socket ridges are commonly reduced, whilst in the Chonetacea they functioned only as socket bounding ridges and the role of body-wall support was filled by the anderidia. The anderidia probably developed from the outer side septa of the Sowerbyellinae and the low ridges dividing the dorsal adductor muscle scars of, for example, *Aegiromena*. An anteriorly prominent dorsal median septum is common to Aegiromeninae and Chonetacea and in both taxa it is believed to have been involved in the support of a simple schizolophe, more or less fused to the dorsal mantle. From the Sowerbyellinae, through the Aegiromeninae and into the Chonetacea there is a reduction in the skeletal support for the teeth. Dental plates are reduced and all

but lost in *Sericoidea*, *Sentolunia* and *Chonetoidea* and are lacking in the Chonetacea. In the ventral interareas of the last two genera Havlíček (1967) has recorded fine canals penetrating the shell substance, as in contemporaneous *Eochonetes*, and these structures are essentially the same as the canals leading from the valve interior into the spines of chonetaceans. All that is required is for the plectambonitacean epithelial evaginations, responsible for the canals, to have retained generative buds at their tips so as to have grown posteriorly beyond the posterior margin. Being generative, in the same way as the rest of the mantle margins, implies the sequential secretion of a protective periostracum followed by mineral deposition around the epithelial cells to form a hollow spine. It is rather as if the epithelial cells of an endopunctum retained a generative tip so that growth, restricted to that local area, continued more or less perpendicular to the valve surface. (This is not to say that I believe in a direct relationship between endopunctae and spines.)

The weakly concavo-convex profile, the outline and external ornamentation of *Sentolunia* and *Chonetoidea* are in accord with the morphology of the first chonetaceans, *Strophochonetes*, and it may be that the strong ventral median rib characteristic of this genus (Pl. 6, figs. 3, 4) is a remnant feature of the Plectambonitacea. In contrast to Boucot & Harper (1968) the present study indicates that *Protochonetes* evolved from *Strophochonetes*. Shell structure studies on the Anopliidae suggest that their origin was in common with other chonetaceans and that this family evolved in the lower to mid-Silurian by morphological differentiation.

In considering the distribution of ancestral stocks and general evolution of the chonetaceans it should be remembered that the present wide geographical separation between the European *Chonetoidea*-like stock and North American *Strophochonetes* would have been less in Upper Ordovician times, if current theories of continental drift and the degree of crustal shortening in the North Atlantic region during the Caledonian orogeny are accepted. In discussing Ordovician faunal provinces Williams (1969) suggested a Caradocian palaeogeography in which oceanic currents would have distributed marine organisms (other factors permitting) in the European and North American provinces. Within the Ashgill of Bohemia, Havlíček (1967) and Havlíček & Vaněk (1966) record several aegiromeninid species morphologically close to the chonetacean ancestor, but no chonetaceans. In the Richmond Series of Anticosti Island, Canada, Twenhofel (1914) only recorded *Plectambonites sericeus* (presumably *Sowerbyella*) with *Chonetes primigenius*. Thus, unless more recent faunal work on Anticosti proves the presence of Aegiromeninae in rocks older than those from which the first *Strophochonetes* are recorded it seems this was not the area in which the evolutionary change took place. Both Aegiromeninae and Chonetacea are found in Girvan, Ayrshire, but the Chonetacea postdate those at Anticosti. It seems possible, therefore, that the evolutionary change took place in the Upper Ordovician within the southern region of Williams' palaeogeographical model.

Using Williams' (1969) model it is suggested that some Bohemian Aegiromeninae, possibly *Chonetoidea* itself, became widely distributed along the southeast margin of the Caradocian seas, perhaps helped by having become epiplanktonic through

their ability to fix to marine algae (Bergström 1968). Within this stock posterior 'hold fasts' retained the ability to secrete shell material, so evolving tissue-filled posteriorly directed spines. Like their ancestors the spat would have been attached by their pedicle to hard material on the sea-floor, or perhaps to seaweeds. However, at an early age the pedicle atrophied and the development of the spines would have helped stabilize benthonic specimens residing in areas subject to marine currents, particularly those specimens facing into the current which were consequently more susceptible to being overturned posteriorly when the shell opened. In a low velocity unidirectional flow from front to back a 'dead water' zone behind the raised dorsal valve might have prevented the burial or erosion of the spines spread out more or less at the sediment to water interface. These adaptations contributed to the evolution of the Chonetacea in the Lower Palaeozoic fine-grained sedimentary environments in which they are commonly found. During Upper Palaeozoic times chonetaceans spread into regions of coarse shelly detritus as well as living in silt and mud environments.

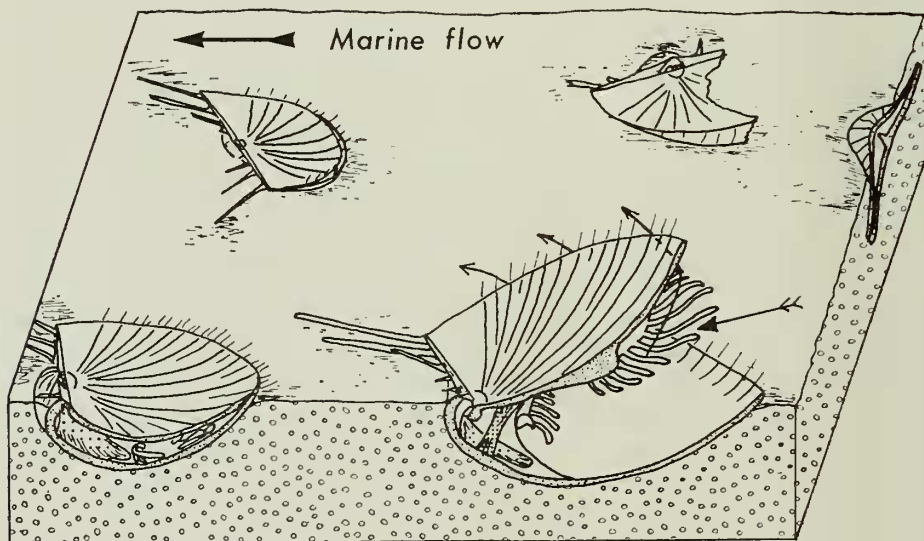


FIG. 8. Hypothetical chonetacean adult community on a soft-bottomed sea floor. The two shells at the top right are dead; one overturned (seen in transverse section), the other part buried. The other three specimens are living (with marginal setae). The two front specimens are cut in longitudinal section; on the left parallel to and on the right along the median line. In these specimens musculature, body wall and lophophore are represented and the arrows indicate the possible flow of water within the brachial cavity.

The spread of chonetaceans to Britain and Europe would have been achieved by Williams' northeasterly oceanic flow, together with the more general break-down in provinciality which started at the close of the Ordovician and became marked during the mid- and upper Silurian.

Representatives of the Chonetacea were the first brachiopods to have developed long tubular spines. Ontogenetic studies of Carboniferous species indicate that these spines normally grew posteriorly at the time of their origin. Thus, in relation to the commissural plane the lateral spines at any particular growth stage were directed posteriorly and were well suited for the support of shells on the substrate. If there was a directional water flow in the environment and if the young shell was able to choose its orientation on settlement it is likely that the water circulatory system outlined above would best have been served by facing into that flow. In this situation posteriorly directed spines are well adapted to the stabilization of the shell (Text-fig. 8).

This demonstration of a gradual change in the shell microstructure from certain Plectambonitacea species to Chonetacea species supports the contention of Williams & Wright (1967) and others that we have here an evolutionary sequence; one which ranges across a subordinal division of the classification in the Treatise. Furthermore, the greater complexity discovered within the skeletal fabrics of these strophomenids allows wider speculation upon phylogenetic relationships and the modification of the relationships suggested by Williams in 1968 and 1970. The phylogenies of the superfamilies presented here (Text-fig. 7) are poorly understood at the points of origin of the Productacea and Thecideacea. Williams (1970) derived the Triplesiacea from the Davidsoniacea which arose from the Billingsellidae. In his view the nisusiid Billingsellacea gave rise to the Orthacea, Clitambonitacea, Gonambonitacea, Strophomenacea and Plectambonitacea.

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Locality details of figured specimens.

PLECTAMBONITACEA

- | | |
|---|--------------|
| <i>Leptestia muscolosa</i> Bekker, Uhaku (C _{1c}) [Upper Llandeilo] Lower Ordovician of Uhaku, Estonia | Plate 5 |
| <i>Lepteloides lepteloides</i> (Bekker), Kukruse (C ₁₁) [Low Caradoc] Upper Ordovician of Kuttejou, Estonia | Plate 5 |
| <i>Sowerbyella (Viruella) liliifera</i> Öpik, Kukruse (C ₁₁) [Low Caradoc] Upper Ordovician of Estonia | Plate 2 |
| <i>Eoplectodonta transversalis</i> (Wahlenberg). Lower Visby Marl, Llandovery, Lower Silurian of Nyhamn, Gotland, Sweden | Plates 1-3 |
| <i>Aegriomena aquila</i> (Barrande), Zahorany Formation [Mid-Caradoc] Upper Ordovician of central Bohemia | Plates, 3, 4 |
| <i>Aegiria grayi</i> (Davidson), Upper Wenlock, Silurian, of Dudley, Worcestershire, England | Plate 4 |
| <i>Sericoidea restricta</i> (Hadding), high Ardwell Group [Upper Caradoc] Upper Ordovician of Craighead, Girvan, Scotland | Plates 4, 5 |

CHONETACEA

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| <i>Strophochonetes primigenius</i> (Twenhofel), Ellis Bay Formation [Ashgill] Upper Ordovician of Mile 5, Jupiter River and Mile 2, 47 Mile Road, Anticosti Island, Canada. (Mile 2 locality is 15-20' above the base of the Ellis Bay Formation: Mile 5 is close to the top junction of the Ellis Bay Formation with the Becscie.) - <i>in lit.</i> TE Bolton, Geological Survey of Canada, Ottawa) | Plates 5, 6 |
| <i>Dawsonelloides canadensis</i> (Billings), Grande Grève Limestone, Siegenian, Lower Devonian of Gaspé, Quebec, Canada | Plate 7 |
| <i>Retichonetes vicinus</i> (Castelnau), Arkona Shale, Hamilton Group. Mid Devonian, ½ ml. upstream from Hungry Hollow Br., 2 ml. E of Arkona, Ontario, Canada | Plates 1, 7 |
| <i>Rugosochonetes silleesi</i> Brunton, high Glencar Limestone, Low D zone Viséan, Lower Carboniferous, of Sillees R, nr. Bunnahone Lough, 2 ml. NW of Derrygonnelly, Co. Fermanagh, N. Ireland | Plates 7, 8 |

STROPHALOSIACEA

- Devonalosia wrightorum* Muir-Wood & Cooper, Lower Ferron Point shale,
Hamilton Group, Mid-Devonian of abandoned Alpena Portland Cement
Co. pit, Alpena, Michigan, USA Plate 8

PRODUCTACEA

- Helaspis luma* Imbrie, Genshaw Formation, Hamilton Group, Mid-Devonian
of Long Lake, 7½ ml. NNE of Alpena, Michigan, USA Plate 9
- Eomarginifera lobata* (J. de C. Sowerby), Great Limestone, E₂ Lower
Namurian of Greenleighton, Northumberland, England Plate 9
- '*Dictyoclostus*' sp, Carwood, Lower Mississippian of 2 ml. SW of Borden,
Indiana, USA Plate 9
- Horridonia horrida* (J. Sowerby), Lower Zechstein, Permian of Trebnitz,
Gera, Germany Plate 9